Title: Comparative urban behaviour of two sympatric columbids: *Columba palumbus* and *Columba livia*

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Abstract

Comparative urban behaviour of two sympatric columbids: Columba palumbus *and* Columba livia. Urban environments favour species tolerant of human disturbance. We compared time budgets and anti-predator behaviour of the common wood pigeon (*Columba palumbus*) and rock pigeon (*Columba livia*) in five urban parks in León (Spain) using video recordings and predator approach tests. The common wood pigeon devoted most time to foraging (81.1%) with moderate vigilance (9.9%), while the rock pigeon showed higher movement (35.25%) and near-absent vigilance (2.95%). It escaped mainly by flying (84%), with greater flight initiation distances (9.47 vs. 4.59 m) and distances to refuge (4.27 vs. 1.89 m). Group size reduced vigilance in the common wood pigeon but only movement in the rock pigeon. These findings show that the rock pigeon exhibits a more habituated, low-vigilance behavioural profile, whereas the common wood pigeon retains a more cautious anti-predator strategy, indicating contrasting responses to urban environments.

Keywords: common wood pigeon, rock pigeon, urban ecology, behavioural ecology, antipredatory behaviour, flight initiation distance.

Introduction

Urbanisation is one of the most pervasive and rapidly expanding forms of land-use change globally, fundamentally transforming natural habitats into highly modified environments characterised by increased human presence, altered resource availability, novel predation pressures, and chronic anthropogenic disturbance (McKinney, 2002; Grimm et al., 2008). These conditions impose strong selective pressures on wildlife, acting as an ecological filter that favours individuals capable of tolerating or exploiting the urban matrix while excluding species with narrower behavioural or ecological tolerances (Blair, 1996; Sol et al., 2005). As a consequence, urban animal communities tend to be dominated by a subset of behaviourally flexible species — the so-called urban adapters — while a large proportion of taxa retreat to less disturbed habitats or experience local extinction (McKinney, 2002; Fontaine & Martin, 2006).

Among vertebrates, birds have emerged as a model system for studying the behavioural consequences of urbanisation, given their diversity, long-standing scientific interest, and the extensive comparative data available across urban gradients (Marzluff, 2001; Chace & Walsh, 2006). A central topic in urban avian ecology is the degree to which species modify their behaviour in response to the predictable, non-lethal nature of human disturbance, a process broadly referred to as habituation (Fernández-Juricic & Jokimäki, 2001). This process is especially evident in anti-predator behaviour: urban birds consistently exhibit reduced escape distances, lower investment in vigilance, and greater tolerance of human approach compared to their rural conspecifics, reflecting a recalibration of perceived predation risk in environments where direct predation threat is reduced (Møller, 2008; Vincze et al., 2016). This reduction in fear responses is one of the clearest examples of urban behavioural convergence, operating both within species across populations and among phylogenetically distant species sharing the same urban environment, and is now recognised as part of a broader process of behavioural homogenisation driven by urbanisation (Mikula et al., 2026). However, these adjustments may also carry costs, as reduced vigilance and altered escape strategies may increase vulnerability in contexts where predation pressure remains high, such as in less urbanised or natural environments. (Lima & Dill, 1990).

Beyond anti-predator behaviour, urbanisation also reshapes time budgets and foraging strategies. The abundance of anthropogenic food subsidies, the spatial predictability of resources, and the reduction in interspecific competition in urban environments can profoundly alter the proportion of time individuals devote to foraging, movement, and social interactions (Shochat et al., 2006). These shifts in behavioural allocation are not uniform across species. Instead, they are expected to vary according to each species' evolutionary history and degree of association with human-modified environments, often described along the urban avoider–adapter continuum (Blair, 1996; Croci et al., 2008). From the perspective of behavioural homogenisation, species that successfully colonise urban environments tend to converge towards similar behavioural profiles, characterised by increased boldness, reduced wariness, and opportunistic foraging strategies, regardless of their taxonomic identity or evolutionary background (Mikula et al., 2026). This convergence implies that sympatric species differing in their degree of urban association may occupy functionally distinct behavioural niches within the same habitat, reflecting their positions along the trajectory of urban behavioural adaptation.

To date, most studies on urban bird behaviour have focused on single species or on comparisons between urban and rural populations of the same taxon (e.g. Møller, 2008; Díaz et al., 2013; Samia et al., 2015). Comparisons between sympatric species differing in their degree of urban association — and thus potentially occupying functionally distinct behavioural niches within the same habitat — remain comparatively scarce (Chace & Walsh, 2006; Croci et al., 2008). Such an approach offers the advantage of controlling for local environmental conditions while highlighting the role of evolutionary and ecological history in shaping behavioural responses to urbanisation (Møller, 2010; Díaz et al., 2013). Here, we present a comparative study of the behaviour of the common wood pigeon (*Columba palumbus*) and the rock pigeon (*Columba livia*) in urban parks of the city of León (Spain), examining both their time budgets and anti-predator strategies. These two species differ markedly in their history of association with humans: the rock pigeon has been domesticated and closely linked to human settlements for centuries (Johnston & Janiga, 1995; Giunchi et al., 2012), whereas the common wood pigeon has colonised urban environments more recently and retains a lower degree of synanthropy (Luna et al., 2024). Specifically, we aim to characterise and compare the behavioural profiles of the two species under comparable environmental conditions, assess interspecific differences in escape behaviour and flight initiation distance, and explore the relationships between movement, foraging, vigilance, and group size within each species. We predict that the rock pigeon, as the more synanthropic species, will invest less time in vigilance, exhibit shorter escape distances, and show a greater reliance on running as an escape strategy (Bocelli et al., 2022; Cooper & Blumstein, 2015), whereas the common wood pigeon will exhibit a more cautious behavioural profile consistent with a species at an earlier stage of urban adaptation (Blair, 1996; Møller, 2010).

Material and methods

Study species

The rock pigeon (*Columba livia*; Gmelin, 1789) is native to the rocky cliff habitats of Europe, North Africa, and South Asia. The Iberian Peninsula constitutes part of its original distribution range, where wild populations associated with coastal cliffs and inland gorges still persist, though their genetic integrity is increasingly compromised by introgression with feral individuals (Fernández-García 2022). Feral populations, derived from centuries of domestication and subsequent re-feralization, are now ubiquitous in Spanish cities, and León is no exception: feral rock pigeons are a permanent fixture of the city's historic centre, plazas, and urban parks, exploiting the ledges and recesses of buildings as functional equivalents of their ancestral cliff habitats (Johnston & Janiga, 1995). Their long commensal history with humans has resulted in a fully synanthropic lifestyle, characterised by year-round breeding, opportunistic foraging on anthropogenic food subsidies, and a strong association with human infrastructure (Giunchi et al., 2012). The common wood pigeon (*Columba palumbus*; Linnaeus, 1758), by contrast, is traditionally a forest and agricultural species that has colonised urban parks and gardens across Spanish cities only in recent decades (Luna et al., 2024). In León, common wood pigeons are now a regular presence in the city's main parks, where they forage and breed year-round, though their urban use remains largely restricted to green spaces with sufficient tree cover. Unlike the rock pigeon, the wood pigeon's foraging strategy relies primarily on tree-derived resources rather than human food waste, and its urban colonisation in Spain is recent enough that it retains ecological traits more typical of woodland populations (Díaz et al., 2013; Luna et al., 2024). This contrast in urban history and degree of association with human settlements makes the two species a particularly suitable pair for comparative behavioural research in urban environments.

Study area

The study was conducted in León, a medium-sized city in north-western Spain founded as a Roman settlement and currently inhabited by just over 120,000 people, with a continental Mediterranean climate characterised by cold winters and warm, relatively dry summers. Our study took place in five urban parks located in the city of León, Spain: Parque de la Granja (42°35'56"N 5°34'01"W), Parque Virgen del Camino (42°35'31.521"N 5°33'29.802"W), Jardín del Chantre (42°35'21"N 5°34'14"W), Parque Dos Hermanas (42°35'20.953"N 5°33'59.556"W), and Jardín de San Francisco (42°35′36″N 5°34′18″W) (Figure 1). All study sites showed heterogeneous habitat composition, including different substrate types, such as stone pathways, sand, grass, and bare soil. This heterogeneity favours the presence of the target species, which are commonly found in these areas.

Sampling protocol

Data were collected between August 2024 and February 2026, and all sampling sessions were conducted between 10:00 and 13:00 h, coinciding with the main period of activity of both species. A total of 25 common wood pigeons (*Columba palumbus*) and 40 rock pigeons (*C. livia*) were sampled. Surveys were performed through active searching by a single observer throughout the study period. At the beginning of each sampling day, we recorded four variables to control for their potential effects on pigeon behaviour: (1) human activity, quantified over a 10-minute period using a mobile application and subsequently converted to persons per minute, (2) temperature (ºC), (3) relative humidity (%), and (4) wind speed (m/s). The temperature was measured by a laser thermometer whereas relative humidity and wind speed were measured using an anemometer.

Upon locating an individual, a photograph was taken for identification purposes and to minimise pseudoreplication. Following this, focal observations were conducted using 6 min video recordings, or until the individual fled or the recording was otherwise interrupted, for subsequent behavioural analysis (ethogram, Table 1). We used BORIS software (Friard & Gamba, 2016) to obtain the duration of each behaviour, in seconds. Once the video recording had ended, a predator approach test was performed to assess the flight initiation distance (hereafter, FID): the observer walked in a straight line towards the pigeon at approximately 0.5 m/s while maintaining direct eye contact (Blumstein, 2006). In addition, the starting distance — defined as the distance at which the observer initiated the approach, a variable known to influence FID (Blumstein, 2006) — was recorded. The escape mode was also noted, as urban birds may choose between running and flying as alternative escape strategies depending on the perceived level of threat (Bocelli et al., 2022). Furthermore, the distance to the nearest refuge was measured, as proximity to shelter may influence both general behaviour and anti-predator responses in these species.

Statistical analyses

Statistical analyses were performed using R software (version 4.3.2; R Core Team, 2023). All statistical tests were conducted at a significance level of $\alpha = 0.05$. When the data did not meet the assumptions of normality and homogeneity of variances, non-parametric tests were applied. Interspecific differences were assessed using the Mann-Whitney U test, both for general behaviour (e.g., time investment across the recorded behavioural categories) and anti-predator behaviour (e.g. starting distance, FID, distance to the nearest refuge). A Chi-square test (χ^2) was used to assess interspecific differences in escape strategy (flying vs. running). Linear regressions were used to examine relationships between continuous behavioural and environmental variables.

Results

No significant interspecific differences were found in any of the environmental variables recorded during behavioural observations, including human presence ($p = 0.761$), temperature ($p = 0.716$), relative humidity ($p = 0.299$), and wind speed ($p = 0.695$).

The behavioural time budgets of the two species differed markedly (Figure 2). The common wood pigeon devoted most of its active time to foraging (median = 81.10%), followed by vigilance (median = 9.90%) and movement (median = 5.00%). In contrast, the rock pigeon allocated a considerably higher proportion of time to movement (median = 35.25%) and a lower proportion to foraging (median = 42.80%) and vigilance (median = 2.95%). Additional behaviours such as preening, resting, aggression, reproduction, and short escape flights were recorded in both species, though they collectively represented a minor fraction of the total time budget (Figure 2). Interspecific differences were statistically significant for all three main behavioural categories: movement (Mann-Whitney U test, $U = 225.5$, $p < 0.001$), foraging ($U = 801.5$, $p < 0.001$), and vigilance ($U = 708$, $p = 0.005$).

Regarding escape behaviour, the two species differed significantly in their choice of escape strategy ($\chi^2 = 17.5$, $p < 0.001$; Figure 3). The common wood pigeon predominantly escaped by flying (84%, $n = 21$), with only 16% of individuals ($n = 4$) choosing to run. The pattern was reversed in the rock pigeon, which escaped primarily by running (72%, $n = 29$), while only 28% of individuals ($n = 11$) took flight. Within the common wood pigeon, individuals that escaped by running were encountered under significantly higher levels of human presence than those that escaped by flying (median running = 10.2 pers/min vs. median flying = 3.6 pers/min; Mann-Whitney U test, $U= 11$, $p = 0.023$), and showed lower vigilance prior to escape (median running = 2.8% vs. median flying = 12.8%; Mann-Whitney U test, $U=70$, $p = 0.041$). No significant differences in FID were found between escape types in this species (Mann-Whitney U test, $U=63$,

$p = 0.132$). Within the rock pigeon, individuals that escaped by flying showed significantly greater FID than those that ran (median flying = 7.1 m vs. median running = 4.15 m; Mann-Whitney U test, $U=253$, $p = 0.005$), suggesting a higher perceived threat in individuals that chose to fly. No significant differences in human presence or vigilance were detected between escape types in the rock pigeon (Mann-Whitney U test, $U=188$, $p = 0.396$ and $U=135.5$, $p = 0.476$, respectively).

With respect to anti-predator escape distances, the common wood pigeon exhibited significantly greater values than the rock pigeon across all three measured variables (Figure 4). Starting distance was significantly higher in the common wood pigeon (median = 15.77 m) than in the rock pigeon (median = 12.08 m; Welch's t-test, $t=2.78$, $p = 0.009$). FID also differed markedly between species (common wood pigeon: median = 9.47 m vs. rock Pigeon: median = 4.59 m; Mann-Whitney U test, $U=796$, $p < 0.001$), as did the distance to the nearest refuge at the moment of escape (common wood pigeon: median = 4.27 m vs. rock pigeon: median = 1.89 m; Mann-Whitney U test, $U=745$, $p = 0.001$).

In both species, movement was negatively associated with foraging time (Figure 5A): common wood pigeon ($\rho = -0.541$, $R^2 = 0.651$, $p = 0.005$) and rock Pigeon ($\rho = -0.551$, $R^2 = 0.362$, $p < 0.001$). The relationship between movement and vigilance, however, differed between species (Figure 5B): no significant association was found in the common wood pigeon ($\rho = -0.019$, $p = 0.929$), whereas in the rock Pigeon a weak but significant negative relationship was detected ($\rho = -0.359$, $R^2 = 0.070$, $p = 0.023$).

Group size had contrasting effects on the behavioural budget of the two species. In the common wood pigeon, larger group size was positively associated with foraging time ($\rho = 0.556$, $R^2 = 0.192$, $p = 0.004$) and negatively associated with vigilance ($\rho = -0.502$, $R^2 = 0.156$, $p = 0.011$). No significant relationship between group size and movement was found in this species (p =

0.182). In the rock pigeon, group size was negatively associated with movement ($\rho = -0.363$, $R^2 = 0.093$, $p = 0.021$), while no significant effects on foraging or vigilance were detected ($p = 0.120$ and $p = 0.199$, respectively).

Discussion

This study reveals marked behavioural divergence between two sympatric columbids occupying the same urban parks in León (Spain). Since they were sampled under similar human presence and environmental conditions, these differences are likely due to their contrasting degrees of synanthropy.

With respect to the time budget, the common wood pigeon devoted the majority of its active time to foraging, with moderate time for vigilance and limited time for locomotion, which is consistent with a stationary, resource-exploitation strategy typical of species still undergoing urban adaptation (Whittingham & Evans, 2004). The rock pigeon showed the opposite profile, characterised by high mobility, reduced foraging, and near-absent vigilance, consistent with a fully synanthropic species that has effectively decoupled alertness from predation risk assessment (Johnston & Janiga, 1995). This pattern has been previously documented in other urban-tolerant passerines such as *Passer domesticus* and *Sturnus vulgaris* (Fernández-Juricic et al., 2002; Lima & Dill, 1990). Together, these differences suggest that the two species occupy distinct behavioural positions along the urban adaptation continuum.

Regarding escape strategy, the two species diverged significantly in their choice of response: the common wood pigeon escaped predominantly by flight, whereas the rock pigeon relied mainly on running, reflecting differences in habitat use and perceived threat level consistent with optimal escape theory, which predicts that prey should select the escape response that maximises survival while minimising the costs of fleeing (Ydenberg & Dill, 1986; Tryjanowski et al., 2016). Escape distances further corroborated interspecific differences in perceived risk: common wood pigeons exhibited significantly greater starting distances (15.77 vs. 12.08 m), FID (9.47 vs. 4.59 m), and distances to the nearest refuge at the moment of escape (4.27 vs. 1.89 m), consistent with the economic escape model, according to which escape decisions depend on the balance between the costs of fleeing and the perceived risk of predation (Blumstein, 2006; Cooper & Blumstein, 2015) and indicative of a higher baseline threat threshold. By contrast, the markedly shorter FIDs of the rock pigeon reflect a substantially lowered threat threshold following long-term habituation to human disturbance, as widely reported across urban bird communities (Møller, 2008; Vincze et al., 2016). Overall, these patterns indicate that the common wood pigeon maintains a more cautious anti-predator strategy, whereas the rock pigeon exhibits a more relaxed response to potential threats in urban environments.

Regression analyses between movement and behavioural categories revealed the obvious trade-off between locomotion and foraging in both species, reflecting the incompatibility of simultaneous movement and feeding. However, movement was negatively associated with vigilance only in the rock pigeon, suggesting a trade-off between locomotion and alertness in this species. By contrast, the common wood pigeon appears to maintain vigilance independently of movement, possibly through intermittent scanning during resource searching (Beauchamp, 2004).

Finally, group size effects diverged markedly between species: in the common wood pigeon, larger groups were associated with increased foraging and reduced vigilance. This aligns with the many-eyes hypothesis and the anti-predator dilution effect, whereby individuals in larger groups benefit from increased collective vigilance and a reduced probability of being targeted by predators (Pulliam, 1973; Caraco et al., 1980), as expected in a species that relies on group-based risk reduction. In the rock pigeon, group size reduced movement but had no effect on foraging or vigilance, suggesting that aggregations in this species reflect resource exploitation dynamics rather than anti-predator coordination (Johnston & Janiga, 1995), which is consistent with a species that has largely decoupled social grouping from predation risk management. Collectively, these results indicate that group formation plays different functional roles in the two species, depending on their degree of adaptation to urban environments.

Taken as a whole, these findings support the urban adapter–avoider framework (Blair, 1996; McKinney, 2002) and reinforce the view that urbanisation acts as a selective filter on behaviour, favouring species capable of adjusting foraging and escape strategies to the chronic, predictable nature of human disturbance in cities (Sol et al., 2005). More specifically, our results show that even closely related species coexisting in the same urban habitat may differ markedly in their behavioural responses according to their degree of synanthropy and history of association with humans. This study therefore highlights the value of comparative within-habitat approaches for understanding how urban environments shape behavioural divergence and adaptation in wildlife. Extending this approach across species and urban contexts will help clarify how differences in synanthropy shape behavioural responses to urbanisation and ultimately determine species success in cities.

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CRediT authorship contribution statement

Iñigo Navidad: Data acquisition, Data curation, Formal analysis, Investigation, Visualization, Writing – original draft. Zaida Ortega: Conceptualization, Formal analysis, Supervision, Writing – review & editing.

Declaration of Generative AI used in the writing process

During the preparation of this manuscript, the authors used ChatGPT and Claude to improve the English language and grammar. The authors reviewed and edited the output as necessary and take full responsibility for the final version of the manuscript.

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Figures and tables

Figure 1: Map of the sampling locations (León, Spain): (A) Parque de la Granja, (B) Parque Virgen del Camino, (C) Jardín del Chantre, (D) Parque Dos Hermanas and (E) Parque San Francisco.

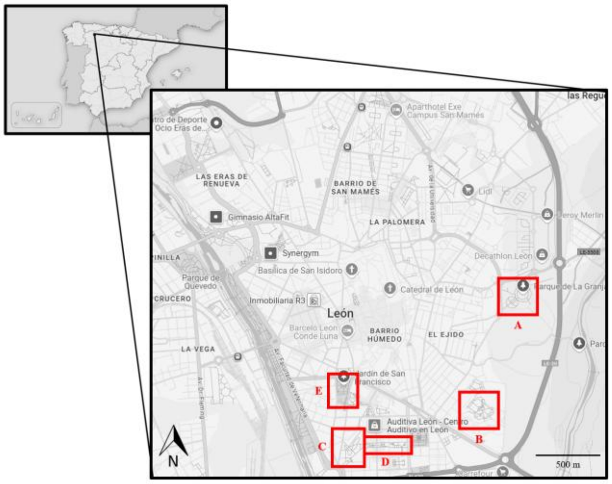


Figure 2: Proportion of time spent by each of the two pigeon species (*Columba palumbus* and *C. livia*) studied in green areas of León (Spain) performing each of the different behaviours (see definitions in the ethogram, Table 1).

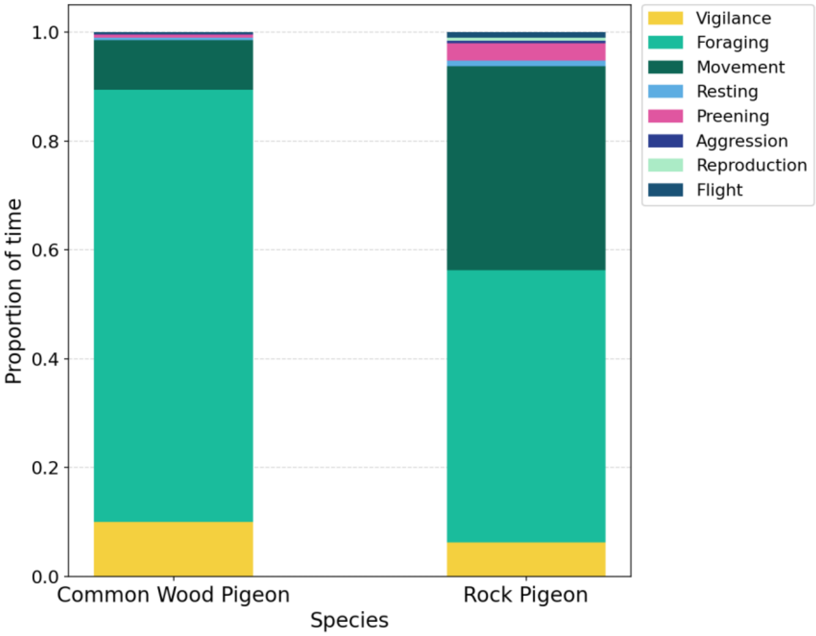


Figure 3: Escape strategy used by the common wood pigeon (*Columba palumbus*, n=25) and the rock pigeon (*C. livia*, n=40) in urban green areas of León (Spain) expressed as the percentage of individuals that chose flying (blue) or running (orange) as their escape response. Statistically significant differences in escape strategy between species were detected using a Chi-square test (χ^2=17.5, p<0.001).

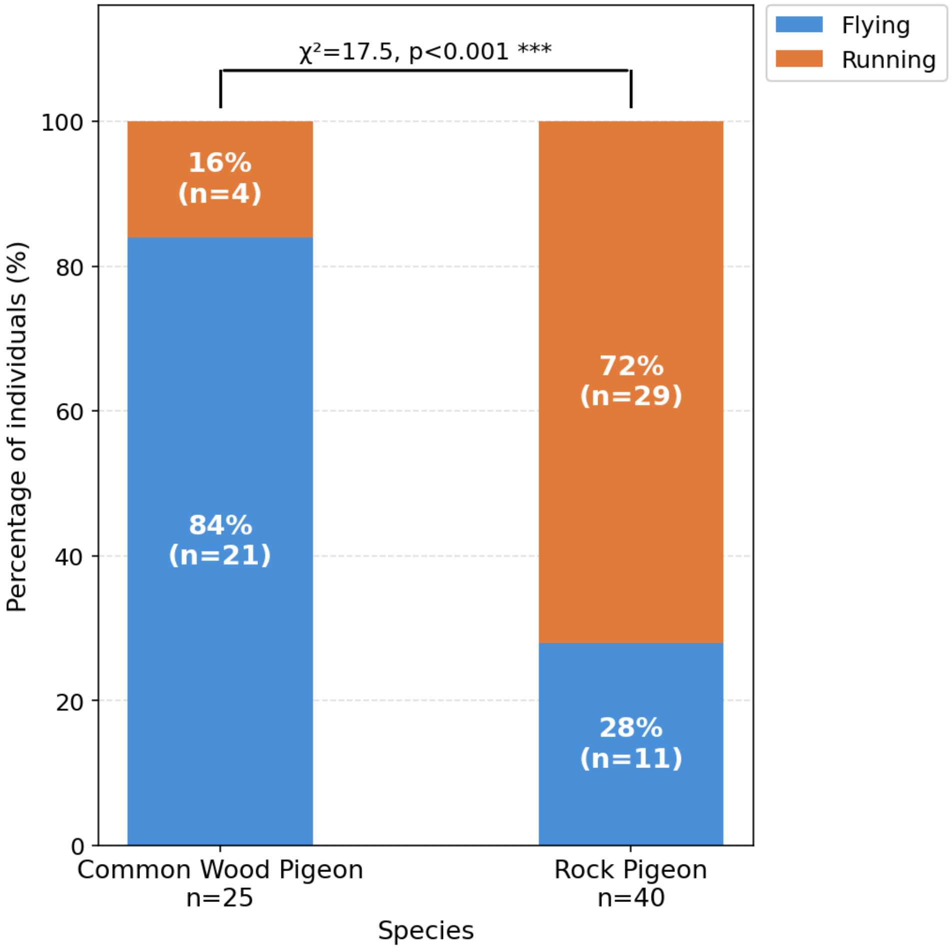


Figure 4: Comparison of escape distances between the common wood pigeon (*Columba palumbus*, n=25) and the rock pigeon (*C. livia*, n=40) in urban green areas of León (Spain): starting distance (A), flight initiation distance (FID; B), and distance to the nearest refuge (C). Significant differences between species were assessed using the Mann-Whitney U test (* p<0.05, ** p<0.01, *** p<0.001).

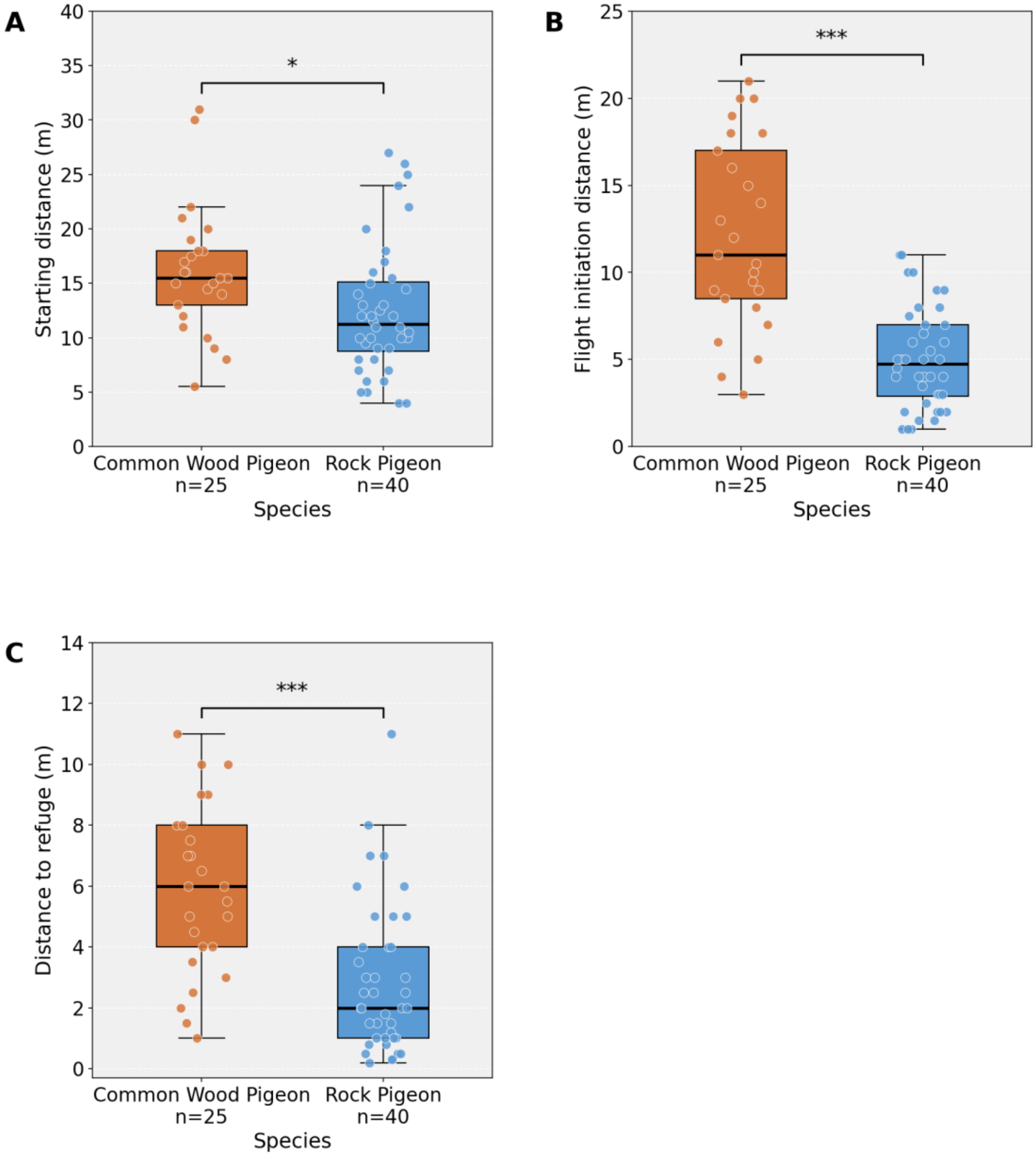
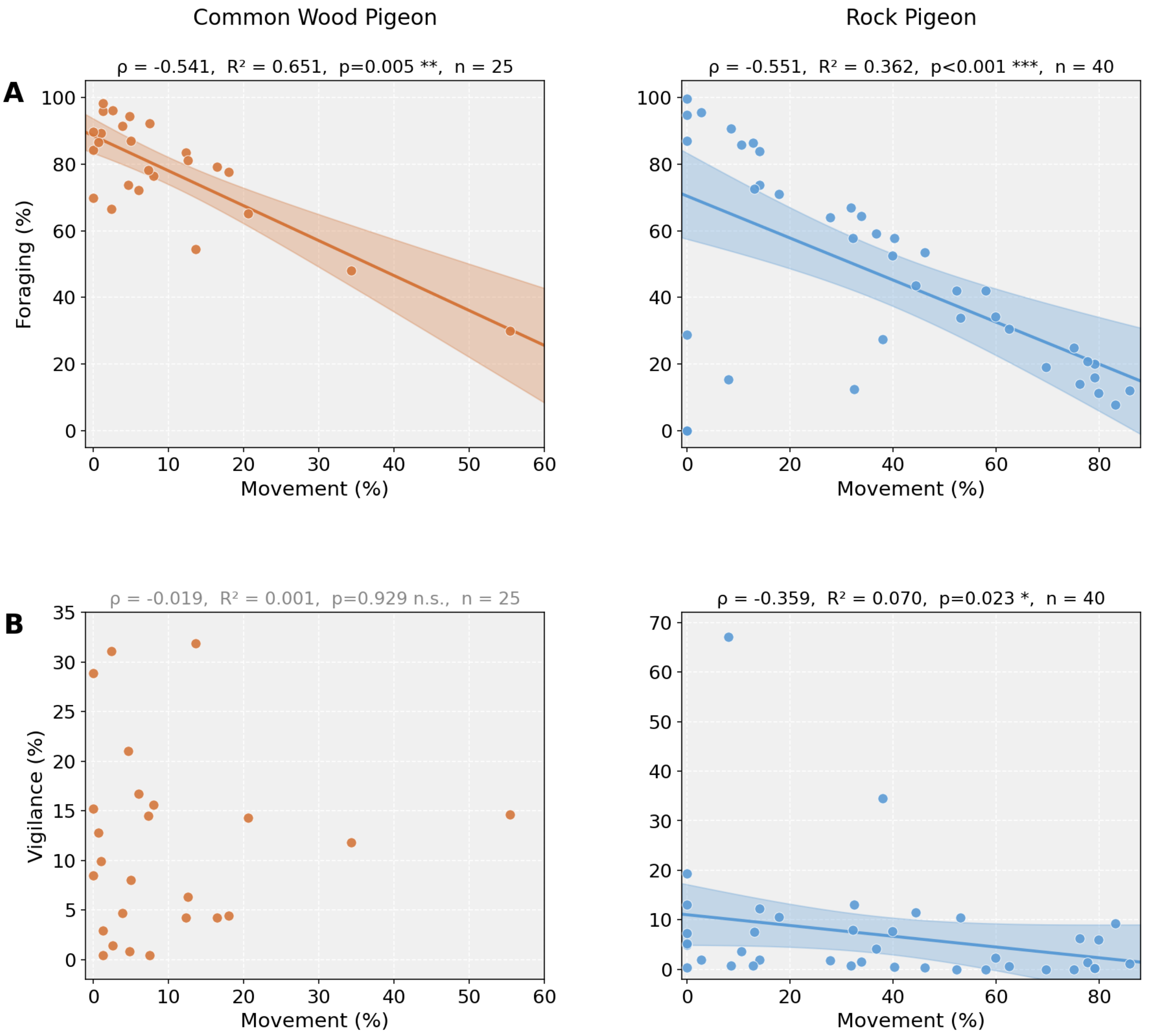


Figure 5: Linear regression analyses between movement (%) and foraging (%) (A), and between movement (%) and vigilance (%) (B), for the common wood pigeon (*Columba palumbus*, n=25, orange) and the rock pigeon (*C. livia*, n=40, blue) in urban green areas of León, Spain. The solid line represents the regression line and the shaded area indicates the 95% confidence interval. Pearson's correlation coefficient (ρ), coefficient of determination (R^2), and significance level are shown above each panel (n.s. = not significant, * $p<0.05$, ** $p<0.01$, *** $p<0.001$).


Common Wood Pigeon
Rock Pigeon
A
ρ = -0.541, R² = 0.651, p=0.005 **, n = 25
ρ = -0.551, R² = 0.362, p<0.001 ***, n = 40
Foraging (%)
100
80
60
40
20
0
Movement (%)
0
10
20
30
40
50
60
0
20
40
60
80
B
ρ = -0.019, R² = 0.001, p=0.929 n.s., n = 25
ρ = -0.359, R² = 0.070, p=0.023 *, n = 40
Vigilance (%)
35
30
25
20
15
10
5
0
70
60
50
40
30
20
10
0
Movement (%)